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A Multiple Regression Model for Predicting the Food Consumption of Marine Fish Populations

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Abstract

The construction of trophic (food web) models of ecosystems, as needed for both theoretical and practical purposes such as fisheries management, requires estimates of food consumption (*Q*) by each of the various species (groups) included in the model. These estimates are usually required on a per-biomass (*B*) basis, i.e. as estimates of the ratio of the food consumed to the weight of the consumers (*Q/B*) during a stated period. For estimates of *Q/B* to be most useful, they must take account of: (*i*) seasonal fluctuations of food intake; (*ii*) the age/size structure of the population; and (*iii*) the type of food consumed.

In this study, 33 estimates of *Q/B* are reviewed, and an empirical multiple regression model for prediction of *Q/B* is presented which incorporates points (*i*) to (*iii*) above. The predictor variables are: (*a*) the asymptotic weight of the fish of the study population, (*b*) the aspect ratio of their caudal fin (as a measure of the average activity and/or metabolic levels of the fish), (*c*) the mean habitat temperature and (*d*) the food type (a dummy variable, 0 in carnivores and 1 in herbivores).

The model explains nearly 75% of the variance in the data set used, which includes myctophids and tunas, flatfishes, rabbitfishes, and other groups from both tropical and temperate waters. The implications of this model for bioenergetics are discussed, along with its future extension, to be based on a much larger data set.

Introduction

Pioneering advances by Ivlev (1945), Steele (1974), and Walsh (1975) put the examination of marine food webs on a rigorous basis. Their work has been expanded upon by various authors (e.g., Jones 1982 and contributions in Longhurst 1981). Two recent developments, moreover, have heightened interest in marine food webs. One was a straightforward method for estimating the equilibrium flows between, and estimating the biomasses of, the various species (groups) involved in a food web from data that are relatively easy to obtain and regularly collected by fisheries research agencies (Polovina 1984; Polovina and Ow 1985). The other development was the series of papers by R. E. Ulanowicz which culminated in his book on flows in marine food webs (Ulanowicz 1986).

These, along with the rich theoretical and empirical data in Platt *et al.* (1981), Pimm (1982) and Fasham (1984) will most probably lead to an explosion of the literature on marine food webs, a good reason to re-examine some of the data used in construction of food-web models.

This paper examines one of the major inputs of 'weighted graphs' (Ulanowicz 1986), i.e. of food webs in which the flows linking a model's boxes are quantified to express the food eaten by the animals in the boxes, along with their average biomass (*B*). This input is the quantity consumed as a fraction of the biomass (*Q/B*) of animals in a box during a nominal period, usually a year. We address the problem of the estimation of *Q* on the

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assumption that the 'content' of a box is a single species of fish; most of what is stated below applies, however, to invertebrates, or the other classes of vertebrates, and/or to groups of similar species lumped into a common box.

Following Polovina (1984), we use *FR* (food required) as the expression for estimates of annual food intake that are used in a model but do not meet our quality criteria for such estimates, and use the expression *Q/B* for estimates which do (see below). Further, we use the term R_d (ration) for the daily food intake, in percentage of live weight, of a single fish.

An examination of the literature cited above and of related studies showed that, in the overwhelming majority of cases, little or no attention is given to the quality of the values of *FR* used for construction of weighted food webs. Particularly, we noted the following:

(*i*) values of R_d, pertaining to a narrow range of fish sizes, are commonly used as input values of *FR*, i.e. treated as if they applied to populations which, however, contain various sizes of fish with very different food consumption;
(*ii*) the values of R_d used often stem from experiments with fish held in captivity and either fed to satiation (which leads to overestimates of consumption in nature) or which were stressed and ate less than they would have in nature;
(*iii*) the values of R_d used as estimates of *FR* apply, more often than not, to a small range of temperatures, i.e. they do not account for the wide, temperature-induced, seasonal fluctuations of food intake observed in natural fish populations;
(*iv*) insufficient attention is devoted to temperature-induced differences between temperate fishes, for which numerous estimates of ration exist, and tropical fishes (even when models of tropical ecosystems are constructed);
(*v*) little or no attention is given to metabolic differences between different species of fishes and hence to their different food consumption.

Materials and Methods

Basic Model for Estimation of Q/B

Pauly (1986) presented a model for the estimation of *Q/B* from growth, mortality and food-conversion data. Slightly simplified, this has the form

$$Q/B = \frac{\int_{t_r}^{t_{max}} \frac{(\mathrm{d}w/\mathrm{d}t)N_t}{K_{1(t)}}\mathrm{d}t}{\int_{t_r}^{t_{max}} W_t N_t} \tag{1}$$

where $N_t \mathrm{d}t$ is the number of fish in the stock aged t to $t + \mathrm{d}t$, W_t is the weight at the age t, $K_{1(t)}$ is the gross food conversion efficiency at age t, and t_r and t_{max} are the ages at entry into and exit from the population, respectively. Fish are assumed to follow the von Bertalanffy growth function (VBGF)

$$W_t = W_\infty[1 - \mathrm{e}^{-K(t-t_0)}]^b \tag{2}$$

where b is the exponent of a length–weight relationship of the form $W = aL^b$ (Beverton and Holt 1957; Gulland 1983; Pauly 1984). Throughout the work leading to this contribution, we have assumed $b = 3$. Following Pauly (1986), the gross food conversion efficiency is assumed to depend on weight (W) according to

$$K_1 = 1 - (W/W_\infty)^\beta \tag{3}$$

where the asymptotic weight (W_∞) is the mean weight of extremely old specimens in a population of fish growing according to the VBGF. [Equation (3) implies that K_1 approaches 1 as W approaches 0; Pauly (1986) presents values of K_1 ranging from 0·74 to 0·93 for fish embryos, which justify the form of equation (3).]

Equation (1) was originally derived for the estimation of Q/B from estimates of gross food-conversion efficiency, defined for a given range of size and a given time interval as

$$K_1 = \text{growth increment/food consumed} \tag{4}$$

from which one can generalize

$$\text{rate of food consumption} = \text{growth rate}/K_1 \tag{5}$$

When different values of K_1 are available from fish held in captivity, they can be combined with an estimate of W_∞ pertaining to a natural population of fish to obtain an estimate of β as defined in equation (3), and the latter then combined with the VBGF to express K_1 as a function of age through

$$K_1 = 1 - [1 - e^{-K(t-t_0)}]^{\beta b} \tag{6}$$

The growth rate of fish can be expressed by the first derivative of the VBGF which, when $b = 3$ (as assumed here), has the form

$$dw/dt = W_\infty 3K[1 - e^{-K(t-t_0)}]^2\,[e^{-K(t-t_0)}] \tag{7}$$

Mortality, in steady-state fish populations is usually modelled using

$$N_2 = N_1\, e^{-Z(t_2-t_1)} \tag{8}$$

where N_1 and N_2 are population numbers corresponding to times t_1 and t_2, respectively, and where Z is the total mortality rate applying to juveniles and young adults, i.e. to that part of the population which contributes to the bulk of a population's biomass.

Under this assumption, $N_t = N_r\, e^{-Z(t-t_r)}$ and, for a steady-state population with constant recruitment, equation (1) can be evaluated for $N_r = 1$, i.e. for a nominal recruitment set at unity, after substituting for W, dw/dt and K_1 from equations (3), (6) and (7) and using as integration limits (t_r, t_{max}) values corresponding to weights that were extremely small (for t_r) and very close to W_∞ (for t_{max}), respectively. [Pauly (1986, fig. 3) showed that Q/B estimates are, within broad limits, insensitive to the specific values of t_r (or W_r), of t_{max} (or W_{max}) and of t_0.]

We have found this model useful not only for estimating Q/B from K_1 values but also to turn published estimates of ration in various fish species into estimates of Q/B for use in models of food webs. We present, in the following, several approaches toward such transformation. We emphasize the estimation of the parameter β, because the other parameters of equation (1) are treated at length in textbooks of fish population dynamics.

Estimation of Q/B from Estimates of Ration

Numerous methods exist for the estimation of ration in free-ranging fish; the most commonly used approaches can be grouped in three classes: (*a*) studies of the dynamics of stomach contents of fish captured in the wild (Bajkov 1935; Sainsbury 1986); (*b*) multiplication of average stomach content by stomach evacuation rate (Elliott and Persson 1978; Pauly *et al.* 1987); and (*c*) indirect estimates derived from oxygen consumption (Winberg 1956; Mann 1978; Mendo and Pauly 1988).

Although widely different in their assumptions and data requirements, these three approaches and their derivatives share the common property of providing size-specific estimates of ration. The computation of a value of Q/B from a single estimate of ration (R_d, see above for definition) is possible in principle. Computations proceed in seven steps, as follows:

(*i*) assemble growth parameters and mortality estimates for the population in question;
(*ii*) adjust available values of R_d such that they account for high consumption during 'summer' and low consumption during 'winter', as can be achieved, for example, by reducing a 'summer' estimate of R_d by a factor accounting for seasonal, temperature-induced differences in metabolic level. (In those cases where ration estimates from temperate fishes were used here to compute Q/B, these had already been adjusted by their original authors. Hence, we give little emphasis to this point. However, it may have to be considered when applying this method to different data sets);
(*iii*) estimate the age (t_a) corresponding to the size for which ration is available (W_a), using

$$t_a = -(1/K)\ln[1 - (W_a/W_\infty)^{1/b}]\,, \tag{9}$$

i.e. the inverse of the VBGF with t_0 set at zero (equation 2);
(*iv*) integrate equation (1) between two values of t, one (t') slightly below t_a, the other (t'') slightly above t_a (i.e., with t' and t'' temporarily replacing t_r and t_{max} as limits for the integration), and with an arbitrary input value of β (e.g. 0·01);
(*v*) compare value of Q/B resulting from (*iv*) with available corrected value of R_d. The two values should be equal since a value of Q/B pertaining to a narrow range of sizes (ages) is equivalent to a value of R_d. If $Q/B > R_d$, redo step (*iv*) with a higher value of β, and conversely if $Q/B < R_d$;
(*vi*) perform step (*v*) until $Q/B = R_d$, and record corresponding value of β;
(*vii*) integrate equation (1) between 0 and ∞ with value of β obtained from step (*vi*).

This iterative approach for estimation of β and Q/B has been described here in some detail because a modified version of this approach is used for cases where more than one estimate of ration is available. [The procedure in (*iv*) to (*vi*) should be replaced, in cases when only one estimate of ration is available, by directly solving equation (3) for β, after setting $K_1 = (dw/dt)/\text{ration}$, and estimating dw/dt from equation (7).]

When several ration estimates are available, step (*i*) is the same as above, while steps (*ii*) to (*iv*) are performed separately for each available, corrected estimate of ration. Then computation proceeds as follows: (*v*) compute sum of squares (SS) of deviations of computed $\ln Q/B$ values from the corresponding $\ln R_d$ values; repeat step (*v*) with different input values of β until SS reaches a minimum, and record corresponding value of β; (*vi*) integrate equation (1) between 0 and ∞ using values of β estimated from step (*v*).

This iterative non-linear approach*, in which the logarithms of the Q/B and R_d values are taken in order to stabilize their variance, is illustrated in Fig. 1, based on data in Daan (1973).

Estimation of Q/B from the Gross Food Conversion Efficiency of Fish Held in Captivity

Pauly (1986) and Pauly and Palomares (1987) presented applications of variants of equation (1) to several populations whose values of β had been estimated from the gross food-conversion efficiency of fish kept in captivity. Essentially, their approach consisted of estimating β and W_∞ from a linearized version of equation (3), of the form

$$\log_{10}(1 - K_1) = \beta\log_{10}W_\infty - \beta\log_{10}W\,, \tag{10}$$

i.e. from a plot of transformed K_1-values against the mean weight of the fish in question.

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*A BASIC program for IBM PC and compatibles, incorporating this and the related routines described below, is available from the authors.

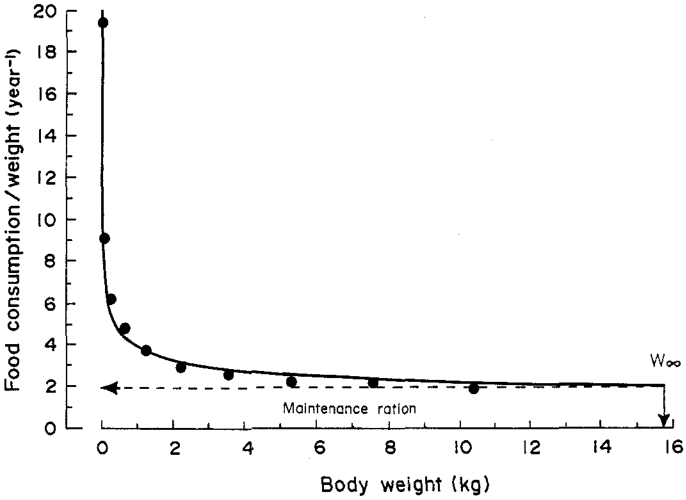

Fig. 1. Relationship between weight (kg) and Q/B (year^{-1}) of North Sea cod, based on estimated weight-specific daily rations (●) taken from Daan (1973).

Pauly (1986) and Pauly and Palomares (1987) showed how equation (10), extended into a multiple regression, can be used explicity to account for differences between the food consumption of fish in captivity and in nature. This approach was used in conjunction with the data analysed here; it should be noted that this approach radically differs from the direct extrapolations from captive to wild fish criticized below.

Data and Models for Empirical Prediction of Q/B

Although the methods presented above considerably simplify the job of estimating Q/B values, we have attempted here to derive preliminary empirical models for prediction of Q/B values, given some easy-to-estimate parameters of a fish population. This was achieved in three steps: (*i*) compilation of a set of 33 Q/B estimates from data readily available in the literature, covering as wide a range as possible of marine fish species and habitats, using the methods described above (see Table 1); (*ii*) identification of variables likely to be good predictors of Q/B in marine fish, with emphasis on variables that are readily quantifiable, and were not directly used in estimating our Q/B values; and (*iii*) estimation of parameters and statistics of various multiple regression models.

Table 1 documents the sources of data used for computing and/or standardizing our 33 estimates of Q/B. Details on computations and conversion factors are given in Palomares (1987)*.

The following variables were retained as predictors of Q/B: (*i*) asymptotic weight, as a measure of the 'size' of the fish of a given population; (*ii*) food type, here coded either 0 (in carnivores) or 1 (in herbivores); (*iii*) mean habitat temperature; and (*iv*) aspect ratio of the caudal fin of the fish of each population as a measure of their activity and/or metabolic levels.

The aspect ratio of the caudal fin (A) of a fish is a dimensionless, species-specific constant defined by

$$A = h^2/s \tag{11}$$

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* Photocopies of this thesis and of a supplementary manuscript incorporating corrections and extensions are available from the authors.

Table 1. Growth and mortality parameter estimates for fish, natural food (or feed used in experiments) and sources of data for all 33 cases studied

Species	L_∞ (cm)^A	K (year^{-1})	t_0 (year)	M (year^{-1})	Food or feed	Sources of growth and mortality data	Source of data on food (type and/or consumption)
Brevoortia patronus	25·3	0·475	−0·36	1·09	Zooplankton, some detritus	Nelson and Ahrenholz (1986), Ahrenholz (1981)	Deegan and Thompson (1985)
Brevoortia tyrannus	40	0·297	−0·52	0·75	Diatoms and zooplankton	Pauly (1978, 1980)	Peters and Shaaf (1981), Durbin and Durbin (1981)
Engraulis encrasicholus	14·3	1·150	−0·17	1·80	Invertebrates and fish larvae	Majarova and Chugunova (1954), Berg *et al.* (1949), Svetovidov (1964)	Sirotenko and Danilevsky (1977)
Hygophum proximum	6·1	0·760	−0·33	2·13	Zooplankton, some detritus	Pauly (1978), Smith and Heemstra (1986)	Gorelova (1984)
Hygophum reindhardtii	7·2	0·540	−0·45	1·61	Zooplankton, some detritus	Pauly (1978), Smith and Heemstra (1986)	Gorelova (1984)
Lampanyctus alatus	7·5	0·500	−0·48	1·53	Zooplankton, some detrius	Pauly (1978), Smith and Heemstra (1986)	Hopkins and Baird (1985)
Myctophum asperum	9·1	0·340	−0·68	1·12	Zooplankton, some detritus	Pauly (1978), Smith and Heemstra (1986)	Gorelova (1984)
Myctophum aurolaternatum	13·0	0·170	−1·28	0·64	Zooplankton, some detritus	Pauly (1978), Smith and Heemstra (1986)	Gorelova (1984)
Myctophum nitidulum	10·3	0·260	−0·85	0·92	Zooplankton, some detritus	Pauly (1978), Smith and Heemstra (1986)	Tseytlin and Gorelova (1978)
Myctophum spinosum	10·9	0·240	−0·94	0·84	Zooplankton, some detritus	Pauly (1978), Smith and Heemstra (1986)	Gorelova (1984)
Symbolophorus evermanni	9·5	0·310	−0·74	1·04	Zooplankton, some detritus	Pauly (1978), Smith and Heemstra (1986)	Gorelova (1984)
Gadus morhua (Baltic)	105·0	0·155	−0·78	0·23	Fish, some crustaceans	Thurow (1974)	Arntz (1974), Bagge (1981)
Gadus morhua (North Sea)	114·8	0·302	0·82	0·20	Worms and molluscs	Daan (1974, 1975)	Daan (1973)
Sebastes melanops	60·0	0·143	−0·99	0·28	Frozen squid and shrimp	Phillips (1964)	Boehlert and Yaklovich (1983)
Epinephelus aeneus	144·0	0·171	−0·08	0·31	*Sardinella* and *Brachydeuterus*	Cury and Worms (1982)	Cury and Worms (1982)
Epinephelus fuscoguttatus	91·7	0·190	−0·66	0·45	Mixed trash fish	Munro and Williams (1985), Wright and Richards (1985), Pagdilao *et al.* (unpublished)	Pagdilao *et al.* (unpublished)

Epinephelus guttatus	—	0·240	−0·20	0·64	Clupeoid fish	Pauly (1986), based on Thompson and Munro (1977)	Menzel (1960)
Epinephelus tauvina	102·0	0·121	−1·38	0·89	Trash fish	Mathews and Samuel (1985)	Chua and Teng (1977, 1979)
Caranx ruber	56·0	0·143	−1·01	0·41	Fish, some shrimps and invertebrates	Garcia-Arteaga and Reshetnikov (1986)	Popova and Sierra (1986)
Coryphaena hippurus	151·0	0·566	−0·18	0·70	Frozen shrimps, squids and fish	Pauly (1978), based on Beardsley (1967)	Hassler and Hogarth (1977), Hagood *et al.* (1981)
Lutjanus campechanus	90·0	0·100	−0·70	0·25	Zooplankton and fish	Jordan and Evermann (1923), Baumariage (1969)	Wakeman *et al.* (1979)
Lutjanus erythropterus	60·0	0·310	−0·44	0·55	*Sardinella* and mixed trash fish	Fable (1980), Brouard and Grandperrin (1984)	Sugama (1982)
Sparidentex hasta	80·6	0·384	0·12	0·35	Pellets	Samuel and Bawazeer (1985)	Teng *et al.* (1980)
Sparus aurata (Adriatic)	59·0	0·275	−0·26	1·00	Sardines, mussels and squid	Audoin (1962)	Kraljevic (1984)
Sparus aurata (SE Medit.)	84·5	0·130	−0·99	0·33	Fish, flesh, soya and wheat	Arias (1980)	Marais and Kissil (1979)
Siganus canaliculatus	25·0	1·870	0·02	2·85	*Enteromorpha*, invertebrates and boiled squash	Pauly (1978), based on Lam (1974)	Carumbana and Luchavez (1979)
Siganus spinus	24·4	3·320	−0·21	3·31	Filamentous algae	Pauly (1978), based on Horstmann (1975)	Bryan (1975)
Thunnus albacares	160·0	0·310	−0·34	0·48	Fish and invertebrates	Hennemuth (1961), Joseph and Calkins (1969), Uchiyama and Struhsaker (1981), Wankowski (1981)	Pauly *et al.* (1987), based on Olson (1981), Olson and Boggs (1986)
Thunnus thynnus	332·0[B]	0·410[B]	−7·00[B]	0·20	Frozen fish	Pauly (1981)	Vincent (1981)
Limanda limanda (♀)	—	0·200	−0·19	0·38	Herring and cod meat	Lee (1972)	Pandian (1970)
Limanda limanda (♂)	—	0·480	−0·27	0·78	Herring and cod meat	Lee (1972)	Pandian (1970)
Pleuronectes platessa (♀)	70·0	0·080	−1·73	0·12	*Mytilus edulis*	Pauly (1980)	Beverton and Holt (1957), Colman (1970), Dawes (1931)
Pleuronectes platessa (♂)	45·0	0·150	−1·02	0·22	*Mytilus edulis*	Pauly (1980)	Beverton and Holt (1957), Colman (1970), Dawes (1931)

[A] All values of L_∞ refer to total length, except for *Thunnus* spp., in which fork length was used.

[B] These parameter values pertain to a 'generalized' form of the VBGF, which has one more parameter (D) whose value was 0·3 in the case reported here (see Pauly 1981).

where h is the height of the caudal fin, and s its surface area, both as defined in Fig. 2 (Lindsey 1978). The use of this variable to quantify the activity level of fishes was derived from the observation that active fishes with high metabolism (and hence high food consumption) such as tuna (Sharp and Dizon 1978) have caudal fins with high aspect ratios, while sluggish fish, presumed to have low food consumption, usually have caudal fins with low aspect ratios. This approach using A as an index of activity level implies: (*i*) that the shape of the caudal fin of fishes was optimized in evolutionary time together with that of the rest of their body and in relationship to their overall physiology; and (*ii*) that the method is applied only to fish with the scombriform mode of locomotion (in which the caudal fin is the main organ of propulsion) and not the balistiform or anguiliform mode (in which other fins or the body as a whole are used for propulsion).

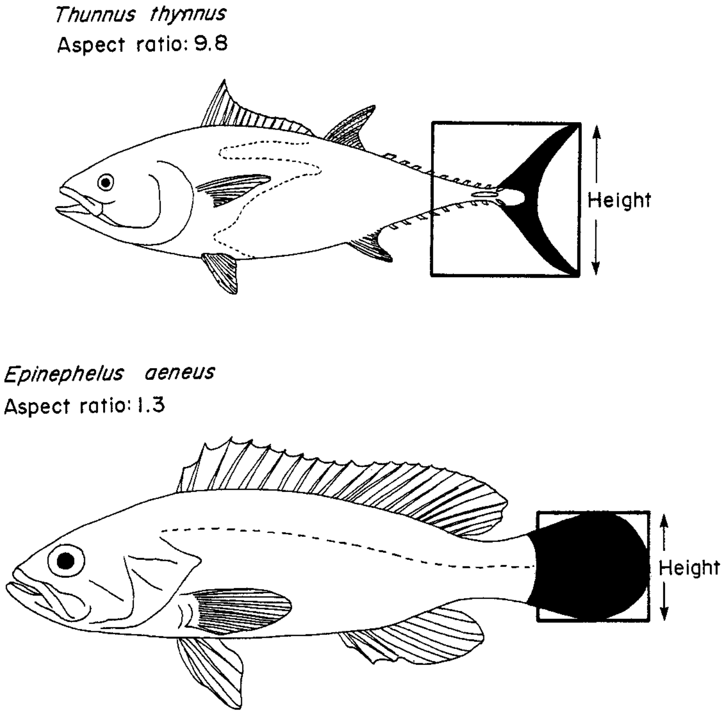

Fig. 2. Schematic representation of method to estimate the aspect ratio ($A = h^2/s$) of the caudal fin of fish, given height (h) and surface area (s, in black).

Results and Discussion

Table 2 presents our estimates of Q/B, along with associated estimates of predictor variables, for the 33 cases included in the present study. As can be seen from this table, our estimates of Q/B range from 0·3 in *Sebastes melanops* (Scorpaenidae) to 16·9 in *Siganus canaliculatus* (Siganidae); the mean sea-water temperatures covered a range of 10 to 28°C, i.e. both temperate and tropical fish are included. Similarly, a wide size range of fish is included, from *Hygophum reinhardtii* (Myctophidae) with $W_\infty = 1$ (g) to *Thunnus thynnus* (Scombridae) with $W_\infty = 622\,000$ (g).

The best predictive model derived from the data in Table 2 has the form

$$\ln Q/B = -0{\cdot}1775 - 0{\cdot}2018 \ln W_\infty + 0{\cdot}6121 \ln T + 0{\cdot}5156 \ln A + 1{\cdot}26 F \qquad (12)$$

where Q/B is the daily food consumption of a fish population as a percentage of its biomass, W_∞ the mean asymptotic (or maximum) weight (g) of the fish in the population in question, T is its mean habitat temperature (in °C) and F its food type (0 in carnivores, 1 in herbivores).

Table 2. Summary of results of case studies, with aspect ratios as defined in Fig. 2, giving estimates of Q/B and associated estimates of predictor variables for 33 species of marine fish

W, weight (g); L, length (cm); Q, food consumption; B, biomass

Species	W_∞[A] (g)	Temperature (°C)	Aspect ratio	Food type[B]	Q/B (% d)
Brevoortia patronus	362	25	1·69	0	2·22
Brevoortia tyrannus	1216	18	2·31	1	8·61
Engraulis encrasicholus	28	15	1·42	0	2·50
Hygophum proximum	2	25	1·65	0	9·28
Hygophum reindhardtii	1	25	1·05	0	6·66
Lampanyctus alatus	2	25	1·62	0	3·32
Myctophum asperum	8	25	1·28	0	10·30
Myctophum aurolaternatum	10	25	1·11	0	4·45
Myctophum nitidulum	11	25	0·93	0	3·28
Myctophum spinosum	13	25	1·28	0	7·38
Symbolophorus evermanni	4	25	1·20	0	5·45
Gadus morhua (Baltic)	12356	10	0·88	0	0·71
Gadus morhua (North Sea)	15714	12	0·88	0	0·62
Sebastes melanops	3776	13	1·31	0	0·30
Epinephelus aenus	47000	19	1·28	0	1·10
Epinephelus fuscoguttatus	12338	28	2·14	0	1·10
Epinephelus guttatus	1880	28	1·44	0	0·76
Epinephelus tauvina	17940	28	1·44	0	0·64
Caranx ruber	3036	27	3·91	0	2·89
Coryphaena hippurus	147000	25	3·29	0	2·32
Lutjanus campechanus	13000	20	1·41	0	1·44
Lutjanus erythropterus	3229	27	2·39	0	1·82
Sparidentex hasta	7400	24	2·18	0	0·64
Sparus aurata (Adriatic)	4000	16	2·84	0	0·44
Sparus aurata (SE Medit.)	9617	24	2·84	0	1·28
Siganus canaliculatus	215	27	2·27	1	16·90
Siganus spinus	234	27	2·42	1	11·50
Thunnus albacares	81920	24	9·26	0	3·19
Thunnus thynnus	622000	15	9·80	0	1·08
Limanda limanda (♀)	756	12	1·20	0	1·01
Limanda limanda (♂)	149	12	1·20	0	1·93
Pleuronectes platessa (♀)	3430	12	1·11	0	0·58
Pleuronectes platessa (♂)	910	12	1·11	0	0·94

[A] The length-weight relationships used for conversion of the L_∞ (in Table 2) to the W_∞ values used here all had an exponent of 3.

[B] 0 in carnivores, 1 in herbivores.

With $R = 0·865$, this model explains nearly 75% of the variance of the data set in Table 2. The standard deviation of the residuals was 0·218 $\log_{10}$ units corresponding to a factor of 1·65 about the predicted values. All estimates of the partial regression coefficients have the expected signs: Q/B increases with temperature, aspect ratio and from carnivores to herbivores, and decreases with size. However, one of the coefficients, that linked with temperature, has a relatively large standard error (see Table 3). We have included it, nevertheless, because its value is close to the value one would expect on physiological grounds.

The parameter Q_{10} expresses the number of times a physiological process runs faster, given a 10°C increase in temperature (Winberg 1956). The Q_{10} concept can also be applied to estimates of Q/B, e.g. for the 10° range straddling the mean temperature in Table 2, i.e. the range 15–25°C. The partial regression coefficient associated with temperature implies, for this range, a value for Q_{10} of 1·4. This is close to the value for Q_{10} of 1·3 for the temperature dependence of natural mortality (and hence predation) that can be estimated from equation (10) or (11) in Pauly (1980).

Table 3. Parameter estimates and statistics of two models for predicting *Q/B* from body weight and other parameters in fish (see text)

Q, food consumption; *B*, biomass

Parameters	Equation (12) estimates	s.e.	*P* (*t*-test)	Caddy and Sharp's model (Equ. 13)
Correlation coefficient	0·865	–	–	0·550
d.f.	28	–	–	10
Intercept	−0·1775	0·5447	–	1·841
ln Weight (g)	−0·2018	0·03291	<0·001	−0·286
Temperature (°C)				0·048
ln Temperature	0·6121	0·3429	<0·1	
ln Aspect ratio	0·5156	0·2016	<0·02	
Food type[A]	1·260	0·3394	<0·001	

[A] Dummy variable, 0 in carnivores, 1 in herbivores.

The partial regression coefficient associated with food type (see Table 3) also has a biologically meaningful value: its antilog of 3·52 is an estimate of the mean nutritive value of animal food for fishes relative to that of plant tissues when both are expressed on the same wet-weight basis. Our preliminary estimate of this parameter, based on only three herbivore species, thus matches the observation of Brett and Groves (1979) that 'the protein fraction of plant diets is frequently one fourth to one third that of meats'. Note that our analysis differentiates only between herbivorous and carnivorous diets, i.e. omnivorous fishes were considered either as carnivorous or herbivorous, depending on the dominant part (in weight) of their diet during the period to which the ration or K_1 values analysed here applied. Our future work will, however, concentrate on methods to express herbivorous, omnivorous and carnivorous diets on the same basis (e.g. N content) and/or approaches to express mixed diets via some combination of dummy variables.

The partial regression coefficient linking Q/B and weight (−0·202) pertains to between-species differences, i.e. it does not express the size-specific decline of Q/B within a population (which is here expressed by the parameter β). Rather, this coefficient corresponds both conceptually and in terms of its absolute value to the 'ecological scaling factor' discussed by Dickie *et al.* (1987) and which was hypothesized to have a value of −0·2.

Figure 3 shows the correlation between empirical and predicted values of Q/B. The even distribution of predicted values on both sides of the 1 : 1 line suggests that predicted values of Q/B should be reasonably accurate.

In this, our model differs from the multiple regression model of Caddy and Sharp (1986) which has the form

$$\ln FR = 1{\cdot}841 - 0{\cdot}286 \ln W + 0{\cdot}048 T \qquad (13)$$

with a value of $R^2 = 0{\cdot}55$. This is based on uncorrected ration estimates compiled by Conover (1978) from reports of experiments with captive demersal fishes generally fed animal food to satiation.

Solving equation (13) for a fish of 1000 (g) and $T = 20$ (°C) gives an estimate of $FR = 2{\cdot}28$; equation (12) on the other hand, solved for $W_\infty = 1000$ (g), $T = 20$, $A = 1{\cdot}5$ (corresponding with a typical demersal fish) and $F = 0$ leads to $Q/B = 1{\cdot}60$, a difference of 70% (the difference of predicted values between the two models is actually larger, because the value of $1{\cdot}60$ refers to a population with $W_\infty = 1000$, i.e. to fish whose biomass and hence also consumption peak at a weight $< W_\infty/3$).

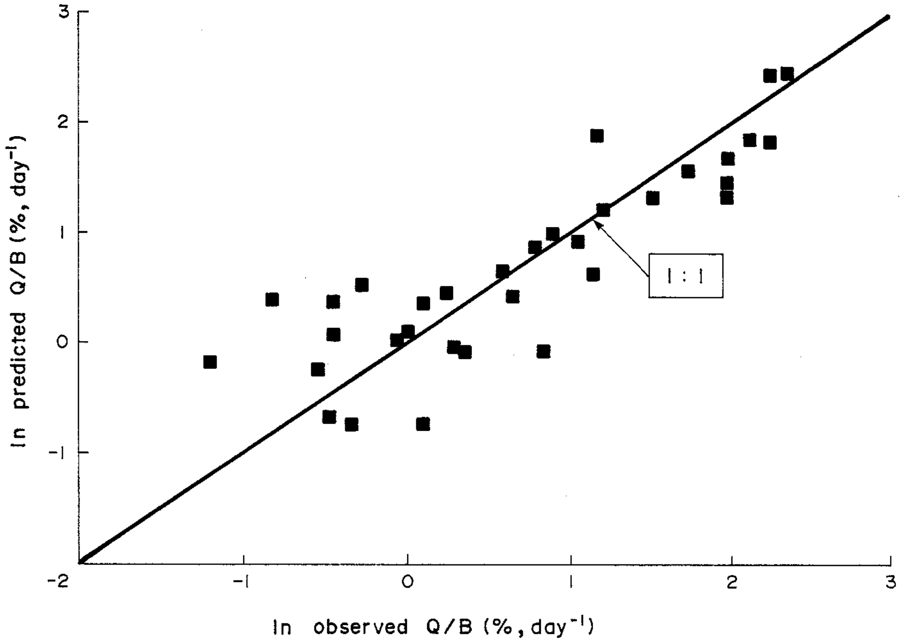

Fig. 3. Estimates of population food consumption predicted by equation (12) *v.* observed values in 33 fish stocks. Note even distribution of points on both sides of the 1 : 1 line.

The present contribution is, to our knowledge, the first in which the aspect ratio of the caudal fin of fishes has been related in quantitative terms with their bioenergetics. It is worth noting here that this parameter, which is extremely easy to estimate (e.g. from photos or drawings of fish), by itself explained 50% of the variance of our set of *Q/B* values.

Although the key features of our newly developed empirical model (equation 12) are encouraging, we consider it necessary to expand the database used here to about 150 cases. This would ensure reduction of the standard errors associated with the various partial regression coefficients, and hence lead to more precise prediction. Moreover, more cases would probably allow the identification of more predictor variables and hence again lead to more precise predictions, and/or allow application of our approach to fishes lacking distinct caudal fins.

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